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AN EXPERIMENTAL INVESTIGATION OF AN APPAR-
ENT REVERSAL OF THE RESPONSES TO LIGHT
OF THE ROACH (*PERIPLANETA*
ORIENTALIS L.).

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Roaches are nocturnal animals, they shun the light and seek the darkness. This has been well known for years; according to Szymanski, Graber¹ is to be credited with thoroughly demonstrating this. According to my observations, it would be incorrect to call this a case of negative phototropism, if we use the term in the sense that Loeb uses it; for there is no orientation to the rays of light, but simply a scampering hither and thither until some dark hole or crevice is found, into which the roach immediately rushes. Normally these roaches are exceedingly shy and any attempt to touch or handle them is responded to by suddenly darting away. Even the slightest touch is sufficient to cause them to run away. In these experiments an attempt has been made to apply the electrical punishment method devised by Yerkes² when experimenting with white mice to a study of the light reactions of one of the common roaches.

HISTORICAL RÉSUMÉ.

To the best of my knowledge, this method has been used only once in the study of insect behavior; that was by Szymanski,³ who has recently made such a study of ten larval cockroaches of the species *Periplaneta orientalis* L. He studied ten male roaches all of the same age. Based on their ability to learn and upon evidences of fatigue, Szymanski classifies roaches as follows; those that with practice make rapid progress and fatigue slowly,

¹ Graber, V., "Grundlinien zur Erforschung des Helligkeits- und Farbensinnes des Tiere," Prag, 1884, pp. 147-157.

² Yerkes, R. M., "The Dancing Mouse," New York, 1907, pp. 98-99.

³ Szymanski, J. S., "Modification of the Innate Behavior of Cockroaches," *Jour. of An. Behavior*, 1912, Vol. II., pp. 81-90.

those that with practice make rapid progress and fatigue rapidly, those that with practice make slow progress and fatigue rapidly. The average number of shocks required to induce a roach to make ten successive refusals to enter the dark chamber was 51, the least 16 and the greatest 118. "Marked individual differences were noted with respect to the time during which the cockroaches retained their newly acquired habit. . . . No relation is evident between the degree of permanency of the newly acquired habit and the number of shocks necessary to establish it." He gives learning curves, each of which he considers a special case of Kraepelin's "Arbeitscurve." He found that animals with amputated antennæ can learn; but, in the case reported, it required 126 shocks to induce it to make ten successive refusals to enter the dark chamber.

APPARATUS AND MATERIAL.

The subjects of these experiments were the following types of the common cockroach (*Periplaneta orientalis* L.): adult females, adult males, larval females one half of an inch long, larval females one fourth of an inch long, adult females with amputated antennæ.

The following apparatus was used: an electric shocking platform, electric batteries, an induction coil, an electrical switch key, and discrimination boxes. Except for certain minor details of construction, the electrical shocking platform is identical with the one used by Szymanski. As used by me the platform consisted of a thick block of wood 28.5 centimeters long and 23.5 centimeters wide, on the top of which two flat copper forks were securely fastened with their tines interdigitating. Each fork had sixteen tines. These tines were 19 centimeters long and 0.8 centimeter wide and each was separated from its neighbors, on all sides, by a space about one millimeter wide. By means of a binding post and wire the handle of each of these forks was attached to one of the terminals of the induction coil, one to each terminal. The induction coil had once been part of a medical battery; the intensity of the shock was regulated by means of a sliding core. Between the battery cells and the induction coil there was a key for making and breaking the circuit.

Three kinds of glass discrimination boxes were used. Box number one was 25 centimeters long, 8 centimeters wide and 8 centimeters deep. By means of transverse glass partitions, this box was divided into three compartments. One partition was stationary, shutting off an end compartment 15 centimeters long. The other partition was adjustable, thus making it possible to vary the lengths of the other two divisions. In these experiments the middle compartment was usually a little less than 4 centimeters long, thus making the other end compartment a little more than 15 centimeters in length. The middle compartment communicated with each of the others by doors which faced each other. Each door was a square 2.5 centimeters long. By means of a special hood and an opaque screen the shape of the transverse partition, one of the end compartments was transformed into a dark chamber. The animal forming the subject of the experiment was placed in that end of the narrow middle compartment which was most remote from the exits. When the animal reached the opposite end of the narrow passage it had an opportunity to select which of the doors it would enter.

After reading Szymanski's paper, which appeared soon after I had begun my experiments, I decided to use a box similar to his. This decision was reached, not because the box described in the above paragraph proved unsatisfactory, but because, on account of the greater freedom, it took longer to perform an experiment with the box I designed than with the one designed by Szymanski. The fact that box number one permitted a roach in one compartment to select which of two others it would enter while Szymanski's box simply permitted it to enter the one towards which it was moving or else remain in the one where it was caused me, at first, to consider this box superior to Szymanski's; but, after much thought, it was decided that box number one was not sufficiently superior to Szymanski's to offset the advantage of shortening the time necessary for conducting an experiment. The shorter the time required for an experiment the less fatigue interferes with the reactions. Then, too, there are other reasons for desiring to shorten the time of intimate contact with these stench-engendering creatures. Box number two was 30 centimeters long, 3 centimeters wide and 8 centimeters

high. One end was transformed into a dark chamber 19.5 centimeters long. Between the dark chamber and the lighted portion an opaque curtain dropped to within 2 centimeters of the floor.

TABLE I.

SHOWING THE ABILITY OF ADULT FEMALE ROACHES TO LEARN TO AVOID ENTERING A SPECIFIC DARK PLACE.

Successive Refusals to Enter the Dark Chamber.	Roach No. 1. An old female that was the subject of these experiments for over thirty-six days. During that time she laid four oöthecæ. During the last three days she was quite feeble. She died soon after the close of the experiments of series O.														
	A	B	C	D	E	F	G	H	I	K	L	M	N	O	Series of experiments. Hrs. elapsed since close of last series.
		8	14	4	21	24	50	4	24	4	120	72	27	40	24
I.	5	5	1	4	10	4	2	8	1	4	0	4	5	6	* Shock paralyzed the
IV.	21	7	4	4	12	4	*	12	11	4	4	8	14	7	roach.
VII.	21	7	4	*	18	9		12	11	4	43	8	16	14	† The roach became too
X.	21	7	5		18	9		12	11	4	43	11	18	†	feeble to react.
	Roach No. 7. One of the quickest to learn of the adult females. These experiments extended over seven days.														
	A	B	C	D	E	F	G	H	Series of experiments. Hrs. elapsed since close of last series of experiments.						
		24	24	24	24	24	24	24							
I.	3	2	2	0	1	0	0	1							
IV.	3	2	2	0	1	0	2	2							
VII.	3	2	2	0	1	0	2	3							
X.	4	2	2	0	1	3	3	8							
	Roach No. 8. One of the most retentive adult females. These experiments extended over eight days.														
	A	B	C	D	E	F	G	H	Series of experiments. Hrs. elapsed since close of last series of experiments.						
		24	24	30	18	24	48	48							
I.	4	0	1	2	0	2	5	12	While series H was being performed the roach was so weak that she could hardly walk.						
IV.	4	0	2	2	0	2	5	25							
VII.	5	0	2	2	1	3	5	25							
X.	5	0	3	2	2	4	5	25							

To help interpret the behavior observed in the other two boxes, box number three was constructed. Like the others it was of glass. It was 25 centimeters long, 8 centimeters wide and 8 centimeters high. A dark chamber 15 centimeters long and of the same width and height as the glass box was placed in one end. In the middle of the partition which separated this dark chamber from the lighted portion of the glass box there was a door 3 centimeters wide and 2 centimeters high.

TABLE II.

SHOWING THE ABILITY OF ADULT MALE ROACHES TO LEARN TO AVOID ENTERING
A SPECIFIC DARK PLACE.

Successive Refusals to Enter the Dark Chamber.	Roach No. 15. This experiment extended over four days. The most apt and the most retentive of all of the adult males examined.				Series of experiments. Hrs. elapsed since the close of last series.
	A	B	C	D	
		24	48	24	
I.	2	0	0	0	
IV.	2	0	0	0	
VII.	3	0	0	0	
X.	3	0	0	0	
	Roach No. 18. This experiment extended over about ten days. One of the dullest males examined. See No. 19.				
	A	B	C	D	Series of experiments. Hrs. elapsed since the close of last series.
		48	4	24	
I.	3	3	6	1	4
IV.	11	5	6	2	4
VII.	13	9	6	2	4
X.	16	9	10	4	5
	Roach No. 19. These experiments extended over about ten days. A very dull roach, one of the dullest males examined. See Ex. 18.				
	A	B	C	D	Series of experiments. Hrs. elapsed since the close of the last series.
		48	24	144	
I.	1	2	4	2	
IV.	11	8	4	3	
VII.	17	8	4	4	
X.	17	11	4	4	
	Roach No. 20. These experiments extended over about four days. One of the aptest males examined. See No. 19.				
	A	B	C	D	Series of experiments. Hrs. elapsed since close of the last series.
		48	2	24	
I.	3	4	0	0	
IV.	3	5	0	0	
VII.	3	5	0	2	
X.	3	7	6	4	

DESCRIPTION OF THE EXPERIMENTS.

The roaches used in these experiments were kept, in solitary confinement, in jelly glasses. A piece of damp sponge supplied the necessary moisture and food was added from time to time. In some cases sand was placed in the bottom of the tumblers. As frequently as necessary the glasses were cleaned. When the time for the experiment arrived the roach was transferred from this jelly-glass to either the middle compartment of box number

one or the lighted portion of box number two. If this was the roach's first experience in the box it immediately rushed into the dark chamber. The current was then turned on and kept on until the roach returned to the lighted portion of the apparatus, when it was immediately turned off. Sometimes the roach would

TABLE III.

SHOWING THE ABILITY OF ONE-HALF INCH LARVAL FEMALE ROACHES TO LEARN TO AVOID ENTERING A SPECIFIC DARK PLACE.

Successive Re- fusals to Enter the Dark Chamber.	Roach No. 2. These experiments extended over thirty-seven days. The quickest to learn of the larvæ of this age.														Series of experiments. Hrs. elapsed since the close of last series.
	A	B	C	D	E	F	G	H	I	K	L	M	N	O	
	4	24	24	96	384	48	96	24	72	24	48	24	24	24	
I.	3	4	2	2	2	1	1	0	0	0	0	0	1	2	* Became paralyzed by the
IV.	4	4	2	2	*	1	1	0	0	1	4	0	1	2	shock.
VII.	4	*	2	2		1	1	0	3	1	4	8	2	2	
X.	4		2	2		1	3	0	3	1	4	8	2	2	
	Roach No. 3. These experiments extended over about forty-six days. Slow to learn, but the most retentive roach of this age.														Series of experiments. Hrs. elapsed since close of last series.
	A	B	C	D	E	F	G	H	I	K	L	M	N	O	
		20	24	240	24	144	72	24	48	24	24	48	24	144	
I.	3	4	4	2	1	0	0	0	0	0	0	0	0	0	* Paralyzed by the
IV.	7	4	4	2	*	2	0	2	2	0	0	0	0	4	shock.
VII.	8	5	8	2		2	0	2	2	0	0	0	0	4	
X.	8	6	8	2		2	0	2	2	0	0	0	0	4	
	Roach No. 4. These experiments extended over about twenty-four days. In aptness and retentiveness an average roach of this age.														Series of experiments. Hrs. elapsed since the close of last series.
	A	B	C	D	E	F	G	H	I	K	L	M	N	O	
		26	22	96	16	72	24	24	24	24	24	48	24	144	
I.	3	0	0	5	2	1	1	1	2	0	1	2	1	1	
IV.	3	5	1	5	3	1	1	1	2	0	1	2	1	1	
VII.	5	5	1	5	3	1	1	1	4	3	4	2	1	8	
X.	5	5	1	5	3	1	1	1	4	3	4	2	1	8	

rush back again, or even several times, into the dark chamber; but, usually, after receiving only one punishment, it would approach the dark chamber more cautiously than before, and if it entered at all did so very slowly, as though expecting something to happen. Sooner or later, on reaching the entrance to the dark chamber, the roach would pause, feel about with its antennæ, then turn about and walk away or else remain there and clean

TABLE IV.

SHOWING THE ABILITY OF ONE-FOURTH INCH LARVAL FEMALE ROACHES TO LEARN TO AVOID ENTERING A SPECIFIC DARK PLACE.

Successive Refusals to Enter the Dark Chamber.	Roach No. 39. These experiments extended over eight days. Slow to learn, but very retentive.								Series of experiments. Hrs. elapsed since the close of last series.	
	A	B	C	D	E	F	G	H		
	24	24	24	24	24	24	24	48		
I.	7	3	1	0	0	0	0	0		
IV.	16	3	1	0	0	2	0	1		
VII.	16	3	1	1	1	2	0	1		
X.	16	3	2	1	1	2	0	1		
Roach No. 40. These experiments extended over fourteen days. Of medium aptness in learning, but not very retentive.										
	A	B	C	D	E	F	G	H	I	K
	24	24	24	24	24	24	24	48	24	144
I.	2	3	1	2	0	2	2	4	2	2
IV.	4	3	13	2	2	4	8	6	2	2
VII.	8	3	13	3	2	5	8	8	2	2
X.	8	3	13	7	2	5	8	8	2	2
Roach No. 41. These experiments extended over eight days. Quick to learn and retentive.										
	A	B	C	D	E	F	G	H	Series of experiments. Hrs. elapsed since close of the last series.	
	24	24	24	24	24	24	24	48		
I.	1	2	1	2	1	0	0	0		
IV.	3	2	1	2	1	0	1	1		
VII.	5	3	1	2	1	0	1	1		
X.	5	3	1	2	1	0	1	1		
Roach No. 13. These experiments extended over fifteen days. Quick to learn, but not very retentive.										
	A	B	C	D	E	F	G	H	I	K
	24	24	24	24	24	24	24	48	24	144
I.	1	3	7	2	1	2	2	0	2	4
IV.	1	4	7	3	2	2	2	2	3	4
VII.	3	4	7	3	2	2	2	2	3	12
X.	6	4	7	3	2	2	2	2	3	12

its antennæ and other appendages. Occasionally it would simply stand there and wave its antennæ. Whenever the roach did not, of its own accord, approach the dark chamber and whenever it paused for some time before the entrance to it, I stroked its back or even gently shoved it towards the darkness. The stroking and shoving was done with a piece of wire the end of which had

been rounded to prevent scratching. Accurate records were kept of the behavior of each roach and of the number of shocks given. Whenever a roach made ten successive refusals to enter the dark chamber the experiment was terminated for that time. Except where I was testing the result of intervals of less than a day, the experiments were conducted at about the same time each day.

Some of the results of these experiments are recorded in the accompanying tables. Although the records of all of the experiments performed have not been tabulated, yet the selected experiments exhibit all of the types of behavior observed. The Arabic numerals in the narrow vertical columns indicate the number of shocks necessary to cause the individual to make the number of successive refusals to enter the dark chamber that is indicated by the Roman numeral in the column to the extreme left. Each shock represents an error made by the roach. For the sake of

TABLE V.

SHOWING THE ABILITY OF ADULT FEMALES WITH AMPUTATED ANTENNÆ TO LEARN TO AVOID ENTERING A SPECIFIC DARK PLACE.

Successive Refusals to Enter the Dark Chamber.	Roach No. 6r. These experiments extended over four days. An average antennaless female.				Series of experiments. Hrs. elapsed since the close of the last series.
	A	B	C		
		24	48		
I.	7	7	2		
IV.	18	7	2		
VII.	18	8	2		
X.	18	8	2		
Roach No. 2r. These experiments extended over ten days. The brightest antennaless female examined.					
	A	B	C	D	Series of experiments. Hrs. elapsed since the close of the last series.
		48	24	144	
I.	2	2	1	2	
IV.	3	4	5	3	
VII.	12	7	5	3	
X.	16	8	5	5	
Roach No. 22. These experiments extended over four days. The dullest antennaless female examined.					
	A	B	C		Series of experiments. Hrs. elapsed since the close of the last series.
		48	24		
I.	2	1	2		
IV.	2	5	3		
VII.	24	11	3		
X.	26	16	3		

uniformity, all of the tabulations were made from experiments performed with box number two.

In every case, sooner or later, the roach always learned to avoid entering the dark chamber; and this was true whether I used discrimination box number one or discrimination box number two. With box number one, where greater freedom was allowed, it usually required more time to establish the habit. As a group adult male roaches learned to avoid the dark chamber more quickly than adult females and young females much more quickly than old females. The slowest of all of the roaches to learn were adult females with amputated antennæ (Fig. 1).

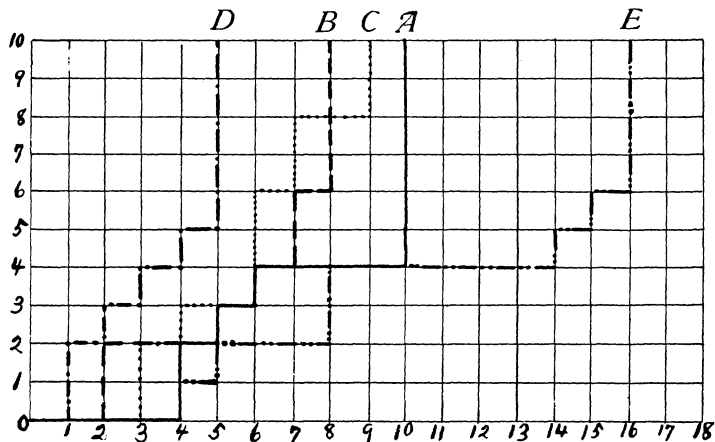


FIG. 1. Learning curves of roaches. Each of these curves represents the average of ten roaches of the kind indicated. The abscissas represent electric shocks, the ordinates the number of refusals to enter the dark chamber that were made before receiving the next shock. A represents adult female roaches; B, adult male roaches; C, larval females one half inch long; D, larval females one fourth of an inch long; E, adult females with amputated antennæ.

There is a marked contrast between the behavior of adult roaches with amputated antennæ and ordinary adults. The normal roach usually moves along the middle of the passageway until it reaches the entrance to the dark chamber, which it either enters or refuses to enter. Before receiving punishment these movements are rapid; after receiving one or more shocks, the roach moves along more slowly and more cautiously. If it approaches the sides at all it is for the purpose of attempting

to climb up them to freedom. On the other hand, the roaches with amputated antennæ move along with a side of the head in contact with one of the side walls of the discrimination box; reminding one very much of a blind person groping along. Usually the movements are rapid, and it requires much punishment to cause the roach to avoid the dark chamber. Indeed, the whole behavior of these antennaless roaches impresses one with the thought that the antennæ play the same prominent rôle in the behavior of roaches that the eyes do in the behavior of man. Other senses are used, but the antennal sense seems to be the one upon which most reliance is placed.

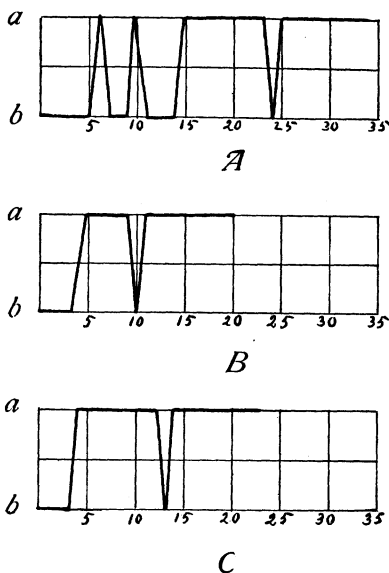


FIG. 2. Reaction curves of three adult females. The numbers represent opportunities to make a choice; *a* represents refusals to enter the dark chamber, *b* represents entrances into the dark chamber.

I stated above that male roaches are more apt than females and that young roaches are more apt than adults. Restricted to the average of each group this assertion is true; but, when we consider individuals as such, we can make no such universal statement. I have encountered males (Fig. 3, *E*) that were much slower to learn than dull females (Fig. 2, *A*) and I have seen larval females that were less apt (Fig. 4, *B*; Fig. 4, *D*) than adult

females (Fig. 2, *A*). The quickest to learn of all of the roaches investigated was a male (Fig. 3, *C*). Ranking next to this male came an adult female with amputated antennæ (Fig. 6, *A*). Indeed the most striking thing in these investigations is the

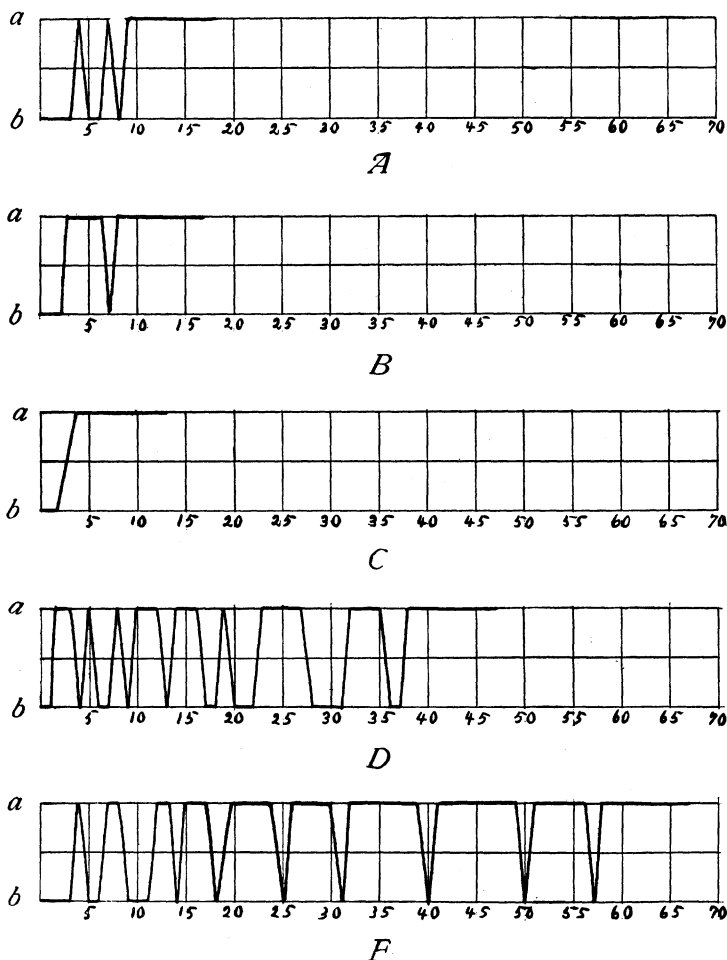


FIG. 3. Reaction curves of five adult male roaches. The numbers represent opportunities to make a choice; *a* represents refusals to enter the dark chamber, *b* represents entrances into the dark chamber.

marked individuality of the roaches. A glance at the few reaction curves published herewith (Figs. 2-6) will serve to emphasize this statement.

Szymanski, in his study of larval male cockroaches, arranged them in three classes: those that learn rapidly and fatigue slowly, those that learn rapidly and fatigue rapidly, those that learn slowly and fatigue rapidly. Arbitrarily I can classify the roaches studied by me in the same manner; but, there are no sharp demarcating lines. It is also possible to divide roaches into

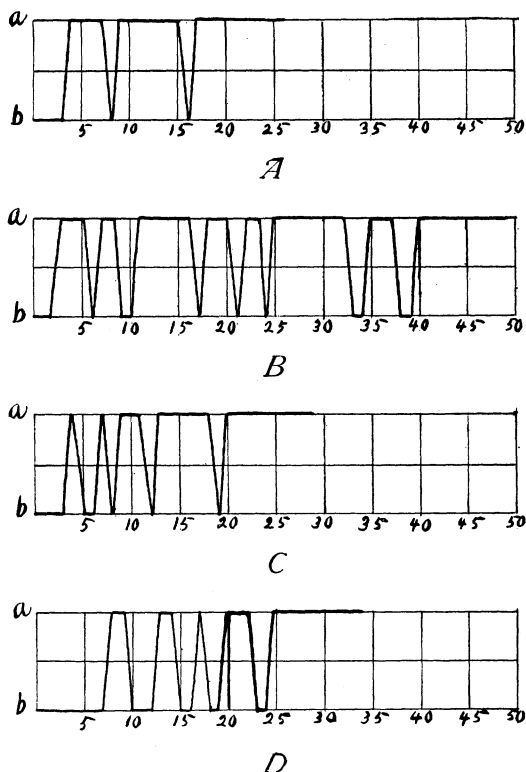


FIG. 4. Reaction curves of four larval females one half of an inch long; *a* represents refusals to enter the dark chamber, *b* represents entrances into the dark chamber.

groups based upon their ability to learn and to retain what they have acquired. Some roaches are quick to learn and retain well what they have acquired (Table I., numbers 7 and 8; Table II., numbers 15 and 20; Table III., number 2; Table IV., number 41); some are quick to learn but not very retentive (Table IV., number 13); some are slow to learn, but retain well what they

have acquired (Table III., number 3, Table IV., number 39); some are slow to learn and not very retentive (Table I., number 1, Table II., numbers 18 and 19); some in learning display mediocre ability but retain well what they have acquired (Table III.,

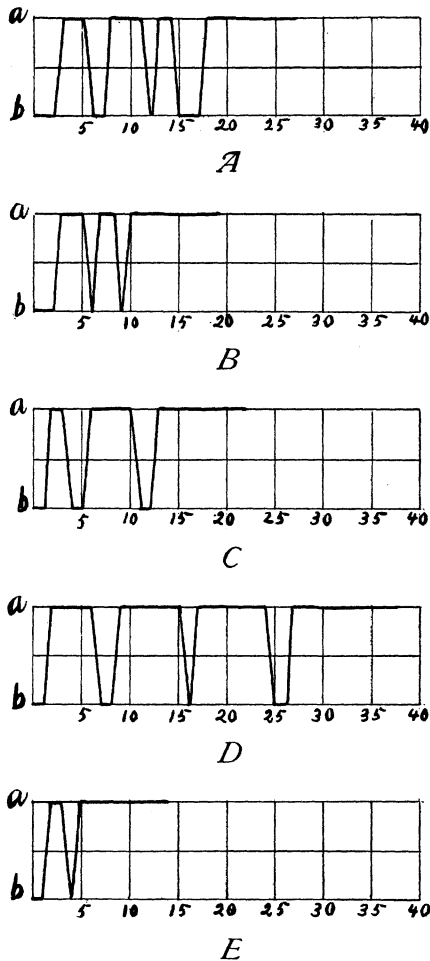


FIG. 5. Reaction curves of five larval females one fourth of an inch long; *a* represents refusals to enter the dark chamber, *b* represents entrances into the dark chamber.

number 4); yet others display mediocre ability to learn and are not very retentive (Table IV., number 41).

Szymanski states that "No relation is evident between the

degree of permanency of the newly acquired habit and the number of shocks necessary to establish it." With this statement my experiments are in accord.

The results of training persist for a long time. Unequivocal evidence of the persistence of the results of training were observed after the following intervals; one day or less (all of the tables),

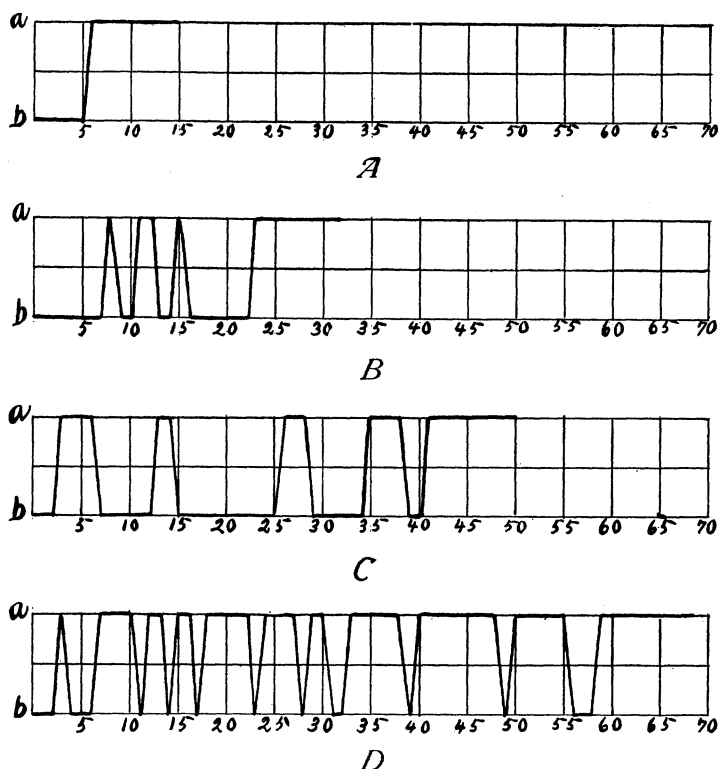


FIG. 6. Reaction curves of three adult females from which the antennæ have been amputated; *a* represents refusals to enter the dark chamber, *b* represents entrances into the dark chamber.

two days (Table II¹, 15*C*, 18*B*, 19*B*, 20*B*; Table III., 2*G*, 2*M*, 3*I*, 3*M*), three days (Table III., 3*G*, 2*K*, 4*F*), four days (Table III., 2*E*), five days (Table I., 1*K*), six days (Table II., 18*E*, 19*D*; Table III., 3*F*, 3*O*), ten days (Table III., 3*D*), sixteen days (Table III., 2*F*), twenty-one days (Table I., 1*G*). Moul-

¹ Throughout this section, the arabic numerals are the numbers of the roaches and the capital letters represent the series of experiments.

ing does not affect the retentiveness of larval roaches. Several of my larval roaches moulted during the progress of these experiments; but, except when the experiment was performed before the body had become sufficiently hard to permit freedom of movement, I never once detected any interference with the retentiveness of the roach. When the health of a roach is impaired and especially when it is dying, there is a marked falling off in its ability to retain the results of experience.

What is the meaning of this refusal of these roaches to enter the dark chamber? Can it be that a few electric shocks have produced such physiological changes in these insects that whereas once they reflexly sought the darkness now they reflexly shun it? Or, is it a case of having learned to avoid a particular dark place on account of certain unpleasant experiences? To find an answer to this question use was made of discrimination box number three. As has been stated above, this was a glass box 25 centimeters long, 8 centimeters wide and 8 centimeters high, in one end of which was a dark chamber 15 centimeters long. The lighted portion of the box communicated with the dark chamber by means of a door 3 centimeters wide and 2 centimeters high. Roaches that had thoroughly learned to avoid the dark chamber were tested in box number two and then transferred, at once, to the lighted portion of box number 3. Immediately such a roach would enter the dark chamber. It was then replaced in the lighted portion of box number 2, where it refused to enter the dark chamber and could not be induced to do so by the method mentioned above. Adult females, adult males, larval females one half inch long and larval females one fourth of an inch long were put through this test. With all such roaches that had thoroughly learned to avoid the dark chamber of discrimination box number two the responses were as stated. Roaches which had not thoroughly learned the refusal reaction and adult females with amputated antennæ, on being returned to the lighted portion of box number two, usually entered the dark chamber. To my mind this test is a conclusive proof that the change in the behavior of these insects is not due to a physiological reversal of the phototropic responses of the roaches; but a case of learning, by experience, to avoid a specific dark place because of certain disagreeable experiences connected with it.

CONCLUSIONS.

1. By means of electric shocks roaches can be trained to avoid entering a specific dark place. This is not a reversal of the phototropic responses of the roaches; but the result of learning to avoid a specific dark place because of certain disagreeable experiences associated with it.

2. Generally speaking male roaches learn more quickly than females and young roaches are more apt than adults; but there are marked individual exceptions to this.

3. In the ability to learn and to retain what they have acquired roaches exhibit marked individuality.

4. Roaches that have acquired the habit of refusing to enter a specific dark place do not lose that habit when they moult.

5. During sickness and just prior to death the retentiveness of the roach is much impaired.

September 20, 1912.